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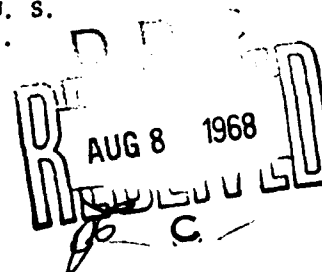
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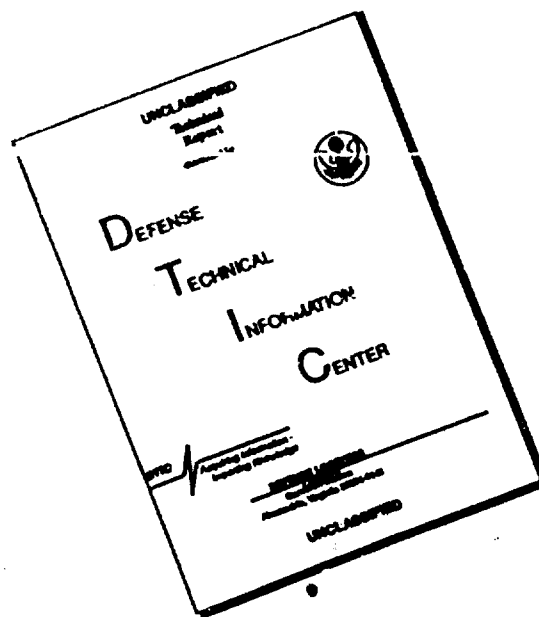


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UNITED STATES ARMY
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The Spread of Puccinia Glumarum Erikss. and Henn. Along the Wheat Head.

by N. A. Maumova

Translated from Trudy Vsesoyuznogo Instituta Zashchity Rasteniy,
pp 155-169, Leningrad, 1958, by SFC Eldon E. Swing, Technical Library,
Technical Information Division.

In the literature about the development of yellow and stripe rust on grains the question about the spread of the rust along the head is completely untouched.

A study of the pattern of the sequence of the rust along the separate spikelets of the wheat head can, to some degree, throw light on the process of rust formation in the seed.

The objects of the anatomical investigation were the seed of the winter wheat Erythrosperrum 61. This variety, which is heavily afflicted by stripe rust, was sown at Prsheval'sk in 1952 in eight planting periods (from 15 Aug to 3 Oct). Samples of the unripe heads were cut simultaneously (14 July) from each planting period.

The vegetational phases of the wheat according to each planting period are presented in composite table 1. In this are noted the dates of the appearance of the rust on the leaves and the character of the head's affliction. A description of the head's affliction is given for the typical cases.

The first planting was made on 15 August. Stripe rust on the leaves was first noted on 1 April, prior to the jointing of the plants.

An irregular spread of the rust along the head was characteristic in the first planting period. Rust in the uredial stage predominated on the flower glumes, and singular telia were encountered on several spikelets (9, 10, 11, 30).

The rust is encountered on the following groups of seeds, beginning from the base of the head: 8-11, 15-19, 26-34. On some of the caryopses there were no symptoms of infection, whereas there were uredia on the flower glumes (spikelets 1, 2, 6, 24).

The rust appeared in two out of three flowers in the form of a mycelium, and uredia had developed in one.

An analysis of rust development on the separate parts of the spikelet and tissues of the caryopses will show new details.

The uredia stand first according to the intensity of the development. They were found in abundance on the flower glumes of all the spikelets, in addition to those situated at the base of the head.

Uredia were also found along the ribs (spikelets 31, 32, 34). They were not on the separate spikelets (3-5, 13, 22, 23, 25, 33). Single telia were found on a few of the spikelets (1, 10, 11, 30). Mature telia had formed only at the 11th spikelet. The mycelium was undetected in one case (spikelet 27).

A profusion of uredia is noted in the fruit coat also, and telia are already embedded; next them is found a many branched mycelium with a protoplasmic content and with numerous nuclei. The telia are immature and small. They are usually situated around the embryo and along the sides of the caryopses. To them are attached traces of granulation that varies in form and size and is enclosed in a gelatinous mass. This granulation is of plant origin and consists mostly of depleted empty plant cells consumed by the fungus. There is a mycelium in the deep tissues of the caryopses and less uredia. Very small incipient telia are found in profusion; they are situated in heaps. One fact represents an exception: incipient uredia and singular telia were embedded into the endosperm and the scutellum where rust is usually not detected.

In one caryopsis (spikelet 29) the telia were only in the fruit coat, protruding outwards from the direction of the crease.

In the crease are a profusion of uredia and telia and a heavily branched mycelium with suckers.

There is a large amount of uredia in the flowers.

Conclusion: 1) the rust had not completed its development cycle, which is proven by the presence of the heavily branched mycelium and the slight representation and immaturity of the telia.

The second planting period was one week later than the first. Tillering occurred a week later than it did with the wheat of the first period. The heading coincided with the wheat of the first period (9-12 June), and the jointing was delayed for four days (1 May). The rust on the leaves of the wheat appeared simultaneously with the first planting period.

Just as on the wheat of the first planting period there is observed an irregular spread of the rust spores along the head. The rust appeared on the first ten spikelets at the base of the head, with the exception of an incompletely developed spikelet (2). In the flower of the 12th spikelet there is only a mycelium. The following three spikelets are clean (13-15). On the next spikelets (16-23) the rust again appears, and rather heavily. There are no symptoms of rust on one of the spikelets among them (18). At the top of the head the last three spikelets are clean, as is the flower situated between them.

Mainly the uredospore formation emerges on the flower glumes, sometimes it is detected only with microscopy. Still another type of uredospore formation falls on the glumes from time to time - uredial heaps (spikelets 4, 16). Telia begin to form at the base of the glumes; on the 10th and 21st spikelets are the teliospores that have been formed.

Rust has formed heavily on the fruit coat. Here it has started the formation of telia. Teliospores have completely formed in the huge pustules. Of particular frequency are the cases of uredia and telia being in the zone that fits over the embryo. Here, near the telia, is developed a thick, branched mycelium (spikelets 5, 8, 9, 10, 16, 20, 21, 23). Sometimes the telia protrude the embryo through the fruit coat (spikelets 10, 16, 21).

Only uredia are encountered in the deep layers of the pericarp, with the exception of one spikelet (17) where telia were detected among a mass of uredia. A strong development of the uredial phase is infrequently encountered (spikelet 6); also infrequent is a profuse development of the mycelium (spikelets 6, 7, 21).

A symmetrical disposition of the uredospore formation is characteristic along the sides of the vascular bundle in the crease of the caryopsis. In one case there were only singular uredia. There was a profuse development of the mycelium in spikelets 6, 9, 10 and 21.

Conclusions: 1) there is an irregular distribution of the rust along the head; 2) the uredial stage predominates; 3) uredial heaps are encountered.

In the wheat of the third planting period the tillering occurred a week later than the tillering in the second planting period. But the jointing and heading of the wheat took place simultaneously with the preceding wheat sowing period (1 May and 8-12 June). The dates of the appearance of rust on the leaves also coincide (9 April).

Almost all of the spikelets have rust symptoms. The spikelets situated at the very base of the head constitute an exception.

There is a succession observed in the change of the fungus's development phases from the base of the head toward the top. There are no symptoms of rust on the first five spikelets. On the following spikelets (6, 7, 8) a mycelium is detected in those tissues where rust is usually found in a form of the known morphological forms. On the next spikelets (9, 10) the rust is already developing in the form of uredia and telia, which are rather scarce. The seed appear clean, but in the fruit coat, and deeper towards the embryo, a mycelium is found. On spikelets 11, 12 and 13 there is already a profusion of telia at the base of the flower glumes. Uredia are situated higher, closer to the upper end of the glume. Telia protrude through the fruit coat in the region of the embryo and crease. Higher on the head (spikelets 14-16) telia are encountered not only at the base of the flower glume, but also in the middle or higher. Telia are found containing formed teliospores that emerge easily from the pustules.

With the exception of one spikelet (17), where the telia had developed insignificantly, one again finds farther in the caryopses a profusion of immature telia, both in the flower glumes and in the fruit coat. Uredia predominate in the crease, but telia are found singularly and are immature (spikelets 18-20).

After a clean flower (spikelet 21) comes a spikelet with clean flower glumes. In the fruit coat, however, there is a mycelium, and deeper, near the embryo and the crease, are situated uredia.

The 24th spikelet is heavily afflicted. Telia have developed in all parts of the caryopsis. Mature telia are established on the flower glumes.

After clean spikelets (25, 26) again follow spikelets afflicted by the rust's uredial stage (27, 28, 31-36). A mycelium is in the fruit coats of these seed. On some of the flower glumes (spikelets 31, 32, 36, 43, 45, 48) the uredial stage is represented by uredial heaps. The uredia in the crease are situated very symmetrically. This quantitative representation correlated also with the qualitative, that is, with the degree of the fungus's maturity. In many of the caryopsis's tissues, both in the fruit coat and then in the inner layer that adjoins the seed coat, and also in the flower glumes the uredial stage was encountered in a lesser number of spikelets than was the telial stage. Thus, in the fruit coat the uredial stage was noted in spikelets 16, 17, 37, 39, 40, 45 and 46; in the deeper layers it was somewhat more and was found in spikelets 18, 19, 20, 22, 27, 29, 31, 32, 36, 41, 42, 43, 48 and 49. In the region of the crease the uredial stage predominates over the telial stage. But, as our preceding investigations have shown, the telial stage in the crease is extremely specific in its morphological characteristics and, evidently, in its genesis.

Conclusions: 1) The sequence in the spread and development of rust along the head is characteristic. 2) The rust's spore development is more profuse and the rust achieves complete ripeness (III stage) on the caryopses in the middle portion of the head and higher. 3) Uredial heaps are in the flower glumes.

In the wheat of the fourth planting period the heading and the appearance of rust on the leaves were noted at the same time as in the wheat of the preceding planting period.

The heads stand out because of the heavy affliction with the yellow rust. All of the flower glumes and caryopses are afflicted, beginning from the base of the head and through to the very tip. A change of the spore development is observed on the heads of this planting period: the fungus has passed through the uredial stage and transformed to the telial stage. Telia are found everywhere: on the flower glumes, on the caryopses and even in the flowers. Mycelia are developing in the flower glumes of singular spikelets (5, 16, 17), and the rest are literally packed with uredia and telia, particularly at the base of the head. The majority of the telia are mature. The uredial stage is sometimes represented by uredial heaps, particularly in the first half of the head (spikelets 1, 2, 3, 5, 6, 7, 9, 10, 11). In the latter two spikelets they are

developed in profusion. The rust has developed weakly in the fruit coat: branched mycelia with suckers predominate (spikelets 2, 3, 10, 11). Uredia are distributed in the inner layers in the direction of the seed coat.

Many uredo-teliopustules are in the crease; they are located separately.

There are many small imperfect seed in the head (spikelets 1, 2, 3, 5, 10, 11, 13, 16, 17).

Conclusions: 1) The rust's spore development broke out along practically the whole head. 2) The rust completed its development cycle. 3) There are both types of uredospore development on the flower glumes, whereupon the uredial heaps predominate. 4) A corallike mycelium is spread through the fruit coat.

In the wheat of the fifth planting period the tillering occurred significantly later - in October, but the jointing almost coincided with the preceding period. The heading occurred two to three days later than the wheat of the preceding sowing periods: 10-14 June. The rust appeared on the leaves very late (28 April).

With small exception, all of the spikelets are afflicted. Uredia and telia are found on the flower glumes of the caryopses situated at the base of the head. A mycelium and uredia are in the fruit coat, but the telial stage is noted on a total of two spikelets (7, 17). All of the rust forms are present in the crease.

In a microscopic section uredospores and a mycelium were detected in one flower on the peduncle.

A lack of rust symptoms on the imperfect caryopses is characteristic, including also the flower glumes surrounding them (spikelets 15, 16).

There are few uredia in the flower glumes located at the base of the head and single telia are visible. Above, there is already a profusion of uredia in the flower glumes (spikelets 5, 9, 10, 13, 14). Uredial heaps are noted in only a single instance (spikelet 12).

We encounter a profuse development of mycelia in the spikelets of the lower portion of the head. Motile microsomes are visible in the mycelia (spikelets 9, 10, 13). The protoplasmic contents of the mycelium are sometimes a pale yellow color instead of being colorless as usual (spikelet 13).

In the crease are the same morphological forms that one begins to encounter in profusion after the 13th caryopsis. The telia, however, are still immature.

The next to the last spikelet to the tip of the head (15) is clean, weakly developed. The neighboring spikelet (16) is also clean.

Conclusions: 1) The rust appeared along the length of the entire head. 2) Of the spore developments the uredial stage predominates. 3) Uredial heaps

are rare. 4) The telial stage is only beginning to develop. 5) A heavily branched mycelium is in the fruit coat. 6) There are no rust symptoms in the imperfect spikelets.

In the sixth planting period a single tillering was noted 2-3 October. Jointing was simultaneous with the wheat of the preceding planting period. Heading also occurred simultaneously with the wheat of the preceding planting period. But the rust appeared on 15 May, that is, later than the jointing.

The spread of the rust along the head is rather unique. The infection includes 1-2 spikelets that are surrounded by clean ones. But practically all of the flower glumes bear symptoms of rust; the exceptions: spikelets 2, 5, 6, 14, and 17. The rust is in the uredial stage. Telia developed on two flower glumes (spikelets 26, 27) and in the fruit coat of a single caryopsis and deeper near the pigmentary layer (spikelet 15). The telia are immature. There were up to twelve flowers that had not developed on the head. Almost all of them are infected. The group of spikelets (9 through 16) in the central part of the head stands out because of the great amount of rust symptoms.

Intervals in the intensity of the rust's development are also noticed along the head. Singular uredial heaps are found on the flower glumes near the base of the head. Starting with the 8th spikelet, their number increases. Farther on the uredial heaps are encountered less and less and at last their number again begins to increase in spikelets 15-19. The telia were immature and were encountered in only three cases.

Conclusions: 1) There is an irregular location of the rust along the head. 2) There is a heavier development of the rust in the middle of the head. 3) The rust had not completed the development cycle (the uredial stage). 4) Uredial heaps predominate.

In the seventh planting period the sprouts emerged from the snow in the spring into two leaves. Jointing occurred at the beginning of May, two days later than the wheat of the preceding period, in which singular tillering was observed after autumn. The wheat began to head simultaneously with the plants of the preceding period. Consequently, the plants already in the jointing stage almost overtook the wheat of the early planting periods. Rust appeared on 22 May.

The rust developed weakly on the spikelets. It is found in the uredial stage on the flower glumes of nine spikelets. A telial-stage formation is noted on only the flower glumes of four spikelets near the top of the head.

There are no rust symptoms on the flower glumes adjoining the empty spikelets (1, 3, 6, 8, 12). Of the nine flowers the rust is only on the flower glumes of two. The uredial stage in the form of uredial heaps predominates (spikelets 15, 19, 20, 23).

The glumes are green, with many chloroplasts in the cells.

The number of caryopses with rust symptoms on the fruit coat or in the deeper layers is still smaller.

Chloroplasts remained in places in the crease and a mycelium with suckers is strongly developed. Uredial receptacles and telia are situated symmetrically alongside the vascular bundle. The telia are immature.

There is a profuse mycelium and even uredo-receptacles beneath the coleorhiza and the pigmentary layer.

We were able to see the start of uredospore formation in the uredial heaps in this material for the first time in the three years we have been conducting anatomical investigations of seed. The spores originate on a mycelium, like chlamydospores (fig 1).

The localization of Puccinia glumarum in the tissues of the flower is presented in figs. 2-9.

Conclusions: 1) There is a weak development of the rust. 2) The uredial stage predominates: the evolution of the telial stage is in view. 3) A mycelium is strongly developed in the crease.

The last sowing was made on 3 October. The sprouts appeared from under the snow in the 1.5-leaf phase almost simultaneously with the sprouts of the preceding period. Tillering was two days late (10 April) and the jointing three days late as compared to the wheat of the preceding period.

The heading occurred simultaneously (13-17 June). The rust appeared on the leaves at the same time as in the wheat of the sixth planting period, i.e., 15 May.

There was a characteristically weak rust development concentrated in the central part of the head. Rust in the uredial stage predominates on the flower glumes; telia are noted on single glumes (spikelets 12-15).

Rust is found in the fruit coat on only five spikelets, and it, too, is in the uredial stage. In one spikelet (17) we detected, for the first time, uredial heaps instead of uredia in the fruit coat, and they were in profusion. Cells with green chloroplasts were retained here. On the grain, uredo-receptacles lie directly on the scutellum and beneath the rootlet. They are symmetrically located along the entire crease. Contrary to usual there are no telia in the crease of the caryopses. Rust symptoms were not found in the flowers (spikelets 3, 6, 9).

Conclusions: 1) The rust is concentrated in the central portion of the head. 2) The rust developed very weakly and is in an early stage of development on the head's flower glumes. 3) There are still fewer symptoms of rust on the surfaces of the caryopses and in the deeper layers, and the formation of telia is not observed. 4) As an exception there was the unique case of finding uredial heaps instead of uredia in the fruit coat of a single caryopsis.

To sum up the anatomical investigations conducted on the spread of rust along the head, many new conditions, which characterize the biological peculiarities of stripe rust, are beginning to appear.

The development of the rust is closely connected to the ontogenesis of the host-plant, and the development of the rust seems as if it follows that of the plant.

This situation is illustrated in graph 1. On it is shown the percentage of spikelets infected in a head with telia on the separate parts for each planting period separately.

Thus, on the wheat of the first two planting periods, which proved to be not completely satisfactory for the development of the plants, the spore development of the rust on the heads is weak and immature (stage II).

In the 3rd and 4th planting periods - optimal for the plants - the rust achieves full maturity (stage III) and profusely covers the head.

There is a profusion of rust in the 5th planting period, but the spore formation is immature.

In the 6th-8th planting periods, in which the tillering of the wheat occurred in the spring rather than the fall - a weak formation of the rust spores is observed, and its development is halted at the formation of uredia.

From here the conclusion is forced upon us that the decisive factor that stipulates the fungus's development are the conditions in which the plant formation occurred in the early stage of the plant's development, and particularly in the tillering phase.

Within the plant itself the development of the rust depends, evidently, on the vitality of the feeding organ. The fungus develops spores more intensively and finishes its development cycle more quickly in the earlier developing and stronger seeds, which occur in the central portion of the head.

In the incompletely matured caryopses the fungus remains at an early stage of development (the mycelium or the uredial stage) and develops spores weakly. The rust does not develop in imperfect caryopses at all.

The character of the rust development on the separate parts of the flower indicates that the infection of the reproductive organs occurs prior to the wheat's flowering.

The intensity and degree of development of the rust on the reproductive organs of the plant correlate with the appearance of rust on the leaves and is not dependent upon the presence of an available air-borne spore infection.

Illustrations

Table 1. The Phenology of Variety *Erythrospermum* 61 according to Planting Periods and the Development of *Puccinia glumarum* on the head.
(Chart headings from left to right) Planting periods; Planting; Tillering; Jointing; Heading; Appearance on the leaves; Affliction of the head.
(/) - weak; (/.../) - median, interrupted; (///) - heavy.

Fig. 1. The formation of uredospores in the uredial heaps (orig.).

In the drawing: a. uredial heap
6. uredospores
6. paraphyses
γ. mycelium

Fig. 2. Uredia in the tissues of two flower glumes, in the ligule, and in the rachis (orig.).

Fig. 3. An unaffected flower. Normal structure of the tissues.

Fig. 4. A flower (afflicted). The flower glumes and the ovary are clean. Uredia are in the rachis near the base of the ovary.

Fig. 5. Uredia at the base of the flower glumes and in the rachis near the ovary.

Fig. 6. The start of telia formation at the base of the ovary.

Fig. 7. Uredia in the flower glumes. A profusion of telia in the rachis at the base of the ovary.

Fig. 8. Localization of telia in the head according to the planting periods.

- | | |
|---------------------|-------------------------|
| 1. the crease | 2. the pigmentary layer |
| 3. the flower glume | 4. the fruit coat. |

Fig. 9. Uredial heaps at the base of the flower glumes. Immature telia are in the tissues of the ligule.